The biogeography of the Aulacocerida (Coleoidea)

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RIASSUNTO

Viene presentata per la prima volta la distribuzione orizzontale e verticale di Aulacocerida (Coleoidea). Gli Aulacoceridi sono stati rinvenuti per la prima volta nel Devoniano inferiore della Europa con la famiglia Protoaulacoceratidae, sconosciuta fuori della Germania. I veri Aulacoceratidi sono stati rinvenuti nel Carbonifero inferiore degli Stati Uniti e segnalazioni sporadiche di questa famiglia si hanno da sedimenti permiani degli Stati Uniti, dall'Asia Sud-orientale e dalla Groenlandia Nord-orientale. Gli Aulacoceridi sono ben noti in affioramenti triassici della Tetide, nelle Alpi, nei Balcani, nell'Indi, Asia Sud-orientale e Nuova Zelanda, sono peraltro noti in affioramenti coevi della Columbia Britannica e degli Stati Uniti Occidentali. La famiglia Xiphoteuthididae compare nel Triassico e coabita con gli Aulacoceratidi in molte regioni tetisiane. Gli Aulacoceridi sono rari nelle regioni settentrionali, ma l'endemico Belemnococeras *e alcuni Xiphoteutidi sono noti nel Canada artico, in Siberia e nelle Spitzbergen. Le Aulacoceratidae sono sconosciute in rocce giurassiche mentre le Xiphoteutide continuano nel Giurassico diventando comuni in sedimenti del Giurassico inferiore di alcune regioni tetisiane, delle coste occidentali americane e penetrando fino nell'Europa Nord-occidentale. Segnalazioni post-giurassico inferiore sono rare e l'ultimo Aulacoceride compare nell'Oxfordiano francese.*

ABSTRACT

The distribution of the Aulacocerida (Coleoidea) is reviewed for the first time. Aulacocerids are first recorded from the Lower Devonian of Europe with the Protoaulacoceratidae, a family unknown outside Germany. The Aulacoceratidae proper are first recorded from the Lower Carboniferous of the United States, and scattered occurrences of the family in Permian sediments are reported from the United States, S.E. Asia and N.E. Greenland. By the Triassic period the aulacocerids were well-established. The Aulacoceratidae are dominant, and are recorded from Tethyan regions in the Alps, the Balkans, India, S.E. Asia and New Zealand, as well as British Columbia, and the western United States. The Xiphoteuthididae first appeared in the Triassic, co-existing with the Aulacoceratidae in most Tethyan regions. Aulacocerids are rare in the northerly regions, but the endemic Belemnococeras *and a few xiphoteuthids are known from Arctic Canada, Siberia and Spitsbergen. The Aulacoceratidae are unknown in Jurassic rocks, but the Xiphoteuthididae continued into the Jurassic, being common in the Lower Jurassic sediments of most Tethyan regions, the west coast of the Americas, and penetrating into northwest Europe. Post Lower Jurassic records are sparse, and the last known aulacocerid appeared in the Oxfordian of France.*

KEY WORDS

Coleoidea Aulacocerida Biogeography - Biostratigraphy

INTRODUCTION

This paper is an attempt to review for the first time the distribution of the Aulacocerida, an order of belemnite-like coleoids which first appeared in early Devonian times. Aulacocerids have a distinctive morphology, but because they possess a rostrum or 'telum' (see Jeletzky, 1966, p. 10), they have previously been included within the Belemnitida by some authors (e.g. see Flower & Gordon, 1959). The discussion of aulacocerid distributions given below is preceded by a discussion of their morphology and an outline of the present state of knowledge concerning their classification. Specimens refered to and figured are housed in the Department of Palaeontology, British Museum (Natural History), London (BMNH) and the Geological Survey of Canada, Ottawa (GSC) unless otherwise stated.

AULACOCERID MORPHOLOGY AND CLASSIFICATION

Aulacocerids are belemnite-like coleoid cephalopods that possess an aragonitic (or organic) rostrum (telum) and distinctive chambered phragmocone (see Dauphin & Cuif (1980) and Dauphin (1982, 1983) for discussion of shell structure). Although superficially similar in appearence to the 'true' belemnites (i.e. to the Belemnitida) the aulacocerids are a distinct group, and it is generally held that the two orders arose from bactritid ancestors (Erben, 1964; Jeletzky, 1966; Jeletzky & Collins, 1986), although some authors (e.g. Steinmann, 1910; Lissajous, 1925; Gustomesov, 1978) have considered the aulacocerids ancestral to the belemnites. The main features that distinguish aulacocerids from belemnites are as follows:

A. Primary features.

1. Aulacocerids lack pro-ostraca and hyperbolar zones, possessing instead a nautilid-like body chamber.

2. The Aulacoceratidae have a ribbed conotheca (with the exception of *Prographularia* and *Stenoconites*, see Jeletzky & Zapfe, 1967). However, the Xiphoteuthididae have a smooth conotheca (Jeletzky, 1966).

3. Aulacocerids possess prochoanitic or achoanitic, rather than retrochoanitic, septal necks in their adult growth stages (after the 10th to 12th septal necks) (Jeletzky, 1966; Jeletzky & Collins, 1986, cf. Bandel, 1985*a*, *b*).

4. The inferred soft-part morphology of the two groups is different. Although both were endocochleate, the mantle cavity of the aulacocerids was within the enclosed body chamber, while that of the belemnites was protected ventrally only by mantle tissue. In addition, Bandel (1985*a*, *b*) has inferred different fin morphology for the two groups, and it is thought that arm morphology was different (hooks on belemnite arms; suckers, etc on those of the aulacocerids; see Jeletzky, 1966; Bandel, 1985*a*).

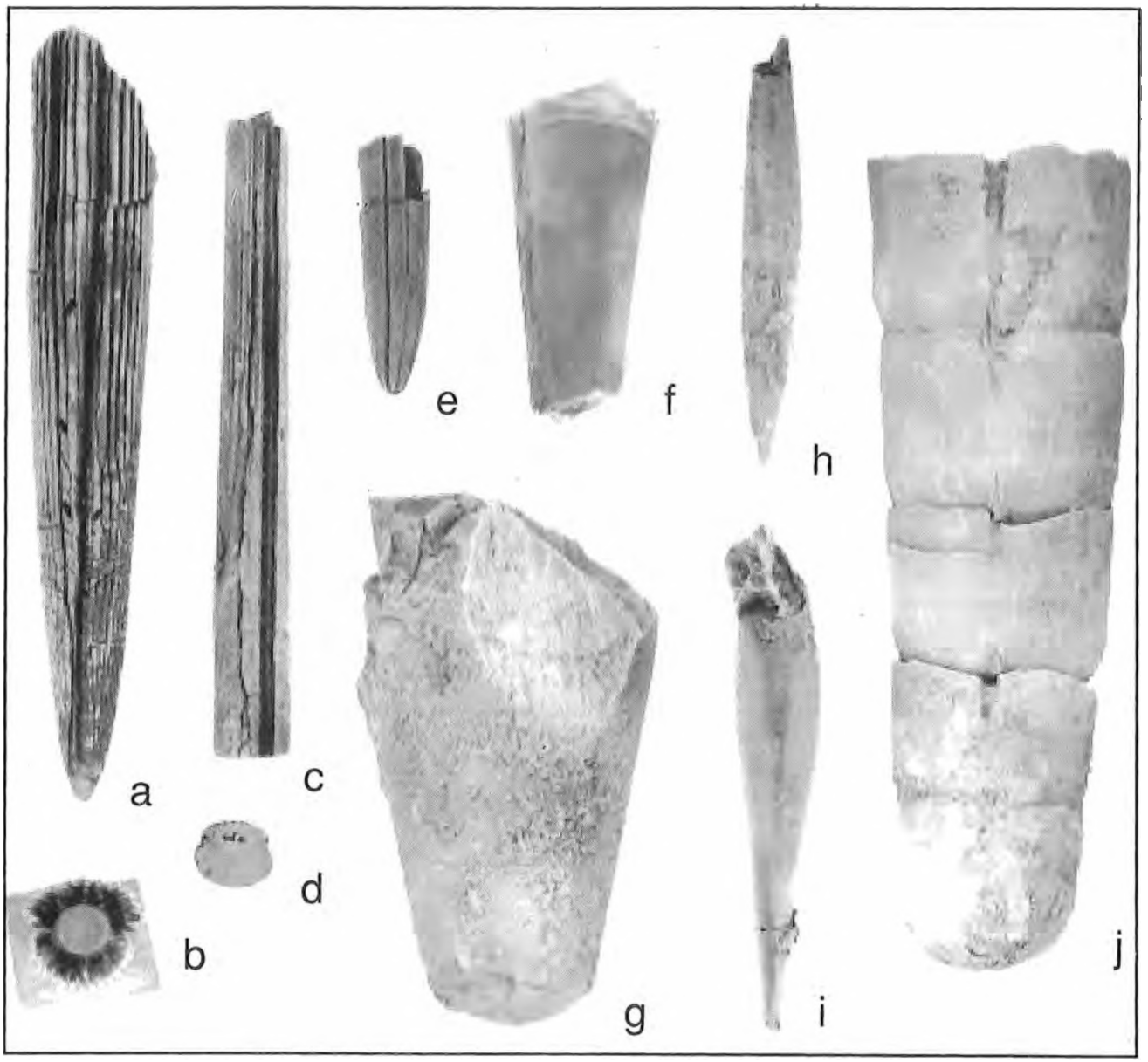


Fig. 1. Representative aulacocerids. 1a-f, Aulacoceratidae. a) *Aulacoceras sulcatum* v. Hauer (BMNH C.59555), lateral view, x1. U. Trias, Nifoekoko, Timor. b) *Aulacoceras sulcatum* v. Hauer (BMNH C. 46512), alveolar section, x1. U. Trias, Cyprus. c) *Buelowiteuthis multisulcata* (V. Bülow) (BMNH C. 59561), lateral view (apex missing), x1. d) transverse section of same specimen, x1. U. Trias, Nifoekoko, Timor. e) *Hematites barbarae* Flower & Gordon (BMNH C. 59560), lateral view, x1. Mississippian (L. Carboniferous), Fayetteville, Arkansas, USA. f) *Dictyoconites (Dictyoconites) reticulata* (v. Hauer) (BMNH C. 5572), lateral view of phragmocone, x1. U. Trias, Rothelstein, Austria. h) *Calliconites sundaicus* (v. Bülow) (BMNH C. 59562), lateral view, x1. U. Trias, Nifoekoko, Timor. i) *Atractites nevadensis* Meek (BMNH C. 59556), ventral view of rostrum, x1. M. Trias, Humboldt Range, Nevada, USA. j) *Atractites* sp. (BMNH C. 46832), ventral view of phragmocone, x1. Domerian (Lower Jurassic), Bakony Mountains, Hungary.

B. Secondary features.

Prior to Jeletzky's (1966) major study, the most important distinguishing features of the aulacocerids were thought to be their relatively long camerae and their relatively acute alveolar angle (e.g. Roger, 1952; Krimgol'ts, 1958; Erben, 1964). However, other coleoid groups with chambered shells have similar alveolar angles and cameral lengths, while some aulacocerids possess short camerae and greater alveolar angles (see Jeletzky, 1966, p. 10). Notwithstanding these problems, long camerae and small alveolar angles are largely characteristic of the group, and in the absence of the features listed above, these characters can be used tentatively to identify its members (e.g. see Dreyfuss, 1957).

The classification of the Aulacocerida used in this paper is given below, based largely on the pre-Treatise work of Jeletzky (1966).

Order AULACOCERIDA Stolley, 1919

Family PROTOAULACOCERATIDAE Bandel, Reitner & Stürmer, 1983

Protoaulacoceras Bandel, Reitner & Stürmer, 1983 (L. Devonian)

Family AULACOCERATIDAE Mojsisovics, 1882

Aulacoceras v. Hauer, 1860 (= *Asteroconites* Teller) (U.

Triassic; text-figs 1a, b)
Buelowiteuthis Jeletzky, 1966 (U. Triassic; text-figs 1c,d)
Prographularia Frech, 1890 (U. Permian-U. Triassic)
Austroteuthis Jeletzky & Zapfe, 1967 (U. Triassic)
Belemnococeras Popov, 1964 [1] (U. Triassic)
Dictyoconites (Dictyoconites) Mojsisovics, 1902 [2] (U. Triassic; text-fig. 1f)
Dictyconites (Actinoconites) Steinmann, 1910 [2] (U. Triassic)
Stenoconites Gordon, 1966 [2] (U. Permian)
Hematites Flower & Gordon, 1959 [3] (L. Carboniferous; text-fig. 1e)
Bactimimus Flower & Gordon, 1959 [3] (L. Carboniferous)
Paleoconus Flower & Gordon, 1959 [4] (L. Carboniferous)

?Family PALAEOBELEMNOPSIDAE Chen, 1982 [5]
Palaeobelemnopsis Chen, 1982 (U. Permian)

Family XIPHIOTEUTHIDIDAE Naef, 1922
Atractites Gümbel, 1861 [6] (= *Xiphoteuthis* Huxley, 1864) (M. Triassic-U. Jurassic) (text-figs 1i,j)
Calliconites Gemmellaro, 1904 (M.-U. Triassic; text-fig. 1h)
Metabelemnites Flower, 1944 (U. Triassic)
Mojsisovcsteuthis Jeletzky, 1966 (?M.-U. Triassic; text-fig. 1g)
Zugmontites Reis, 1907 (M. Triassic)

Family CHITINOTEUTHIDIDAE Müller-Stoll, 1936
Chitinoteuthis Müller-Stoll, 1936 (L. Jurassic)

AULACOCERID BIOGEOGRAPHY

1. *Palaeozoic records* (text-fig. 2). Records of Palaeozoic aulacocerids are very sparse. The earliest known aulacocerid is apparently *Protoaulacoceras* from the Lower Devonian Hunsrück Shale of Hunsrück (Rheinland Palatinate), West Germany. Bandel *et al.* (1983) included this genus in a new family, the Protoaulacoceratidae, which is as yet unknown outside Germany. The first record of the Aulacoceratidae may be a single dubious specimen from the Upper Devonian of Belgium (de Koninck, 1843) but the illustrated specimen is too poor to be reliable. The first definite Palaeozoic records of this family are from the Lower Carboniferous of the United States, and three genera, namely *Hematites* (the most abundant), *Bactrimimus* and *Paleoconus*, were described by Flower & Gordon (1959) (see also Gordon, 1966*a*) from Utah and Arkansas.

There are slightly more Permian that earlier Palaeozoic records. Dawson (1978) described an indeterminate aulacocerid (BMNH C. 46902) from the Lower Permian of Thailand. This specimen is represented by a fragment of a smooth, slightly compressed or depressed rostrum enclosing an infilled (with fine sediment) alveolus, the phragmocone itself being lost. The alveolus appears to have penetrated the majority of the rostrum, and the alveolar angle is small (approximately 5°). Thin sections reveal that the rostrum was built of smooth, concentric layers without 'bundles', rather like that of a belemnite. The smooth surface of the rostrum in this specimen does not allow direct comparison with other Permian aulacocerids, and its taxonomic situation is unclear. Gordon (1966*b*) described a new genus *Stenoconites* (Aulacoceratidae) from the Upper Permian of Idaho and Montana, and Chen & Sun (1982) have subsequently recorded this genus from China. These authors also described a new family from China, the Palaeobelemnopsidae, occurring there with *Stenoconites*. The Palaeobelemnopsidae are a family (originally included in the Belemnitida, see above) of aulacocerids with hastate, grooved rostra that are unknown outside China (Chen & Sun, 1982). Locally abundant (often in 'battlefield' accumulations) in the Upper Permian sediments of N.E. Greenland is *Prographularia groenlandicus* (Fischer) (Fischer, 1947), the first record of a genus which continued into the Upper Triassic (Jeletzky & Zapfe, 1967). Also recorded from the Permian of East Greenland is an unnamed genus with affinities to *Aulacoceras* (Jeletzky, 1966, Pl. 6, fig. 2). This specimen (Greenland Geological Survey GGU 20305) is slightly crushed, but shows relatively coarse 'ornament' with an apparently thin rostrum covering a penetrative phragmocone.

In summary, although Palaeozoic records of Aulacocerida are sparse, they do indicate that the order had appeared at least as early as Devonian times, the Aulacoceratidae proper being clearly recognisable in the Carboniferous. There are no definate records of the Xiphoteuthididae in the Palaeozoic, although Gordon (1966*b*) has assigned *Paleoconus* to this family.

2. *Triassic records* (text-fig. 3). Aulacocerids are well-know in the Triassic, especially from regions like Timor (e.g. v. Bülow, 1915) and the Alps (e.g. Mojsisovics, 1882). However, there are few records of either Aulacoceratidae or Xiphoteuthididae known from the Lower Triassic (Bülow-Trummer, 1920; Jeletzky, 1966), the maximum amount of data being available for Upper Triassic occurrences.

In the mid-Triassic, the aulacocerids had already become widespread in distribution, with reported occur-

1. Jeletzky (1966) previously considered *Belemnococeras* a synonym of *Metabelemnites* Flower, but now recognises its generic autonomy (J.A. Jeletzky pers. comm., 1987) although reassigning it to the Aulacoceratidae because of its distinct growth pattern (see Dagys & Nal'nyaeva, 1987, pl. 16-18).

2. Included by Gustomesov (1978) in his family Dictyoconitidae.

3. Included by Gustomesov (1976) in his family Hematitidae.

4. Included in the Xiphoteuthididae by Gordon (1966*b*), and the Hematitidae by Gustomesov (1976).

5. Originally included by Chen & Sun (1982) in the Belemnitida. Phragmocone characteristics (Chen & Sun, 1982, text-fig. 4) suggest that assignment of the Palaeobelemnopsidae to the Aulacocerida is more correct, although its familial autonomy is in doubt. Zhu & Bian (1984) also record 'true' belemnites from the pre-Jurassic sediments of China. However, the position of this family, the Sinobelemnitidae, cannot be evaluated without detailed study of the actual specimens, although it is possible that they may represent a distinct aulacocerid family, as some members of the Xiphoteuthididae closely resemble 'true' belemnites (e.g. *Metabelemnites*).

6. Flower (1944) erected the genus *Ausseites* as a replacement name for those *Atractites*-like phragmocones without rostra preserved. Although a great many recorded *Atractites* are phragmocones only, Jeletzky (1966) following Kühn (1965) determined that *Ausseites* is a synonym of *Atractites* because its type species has a typical *Atractites* rostrum.

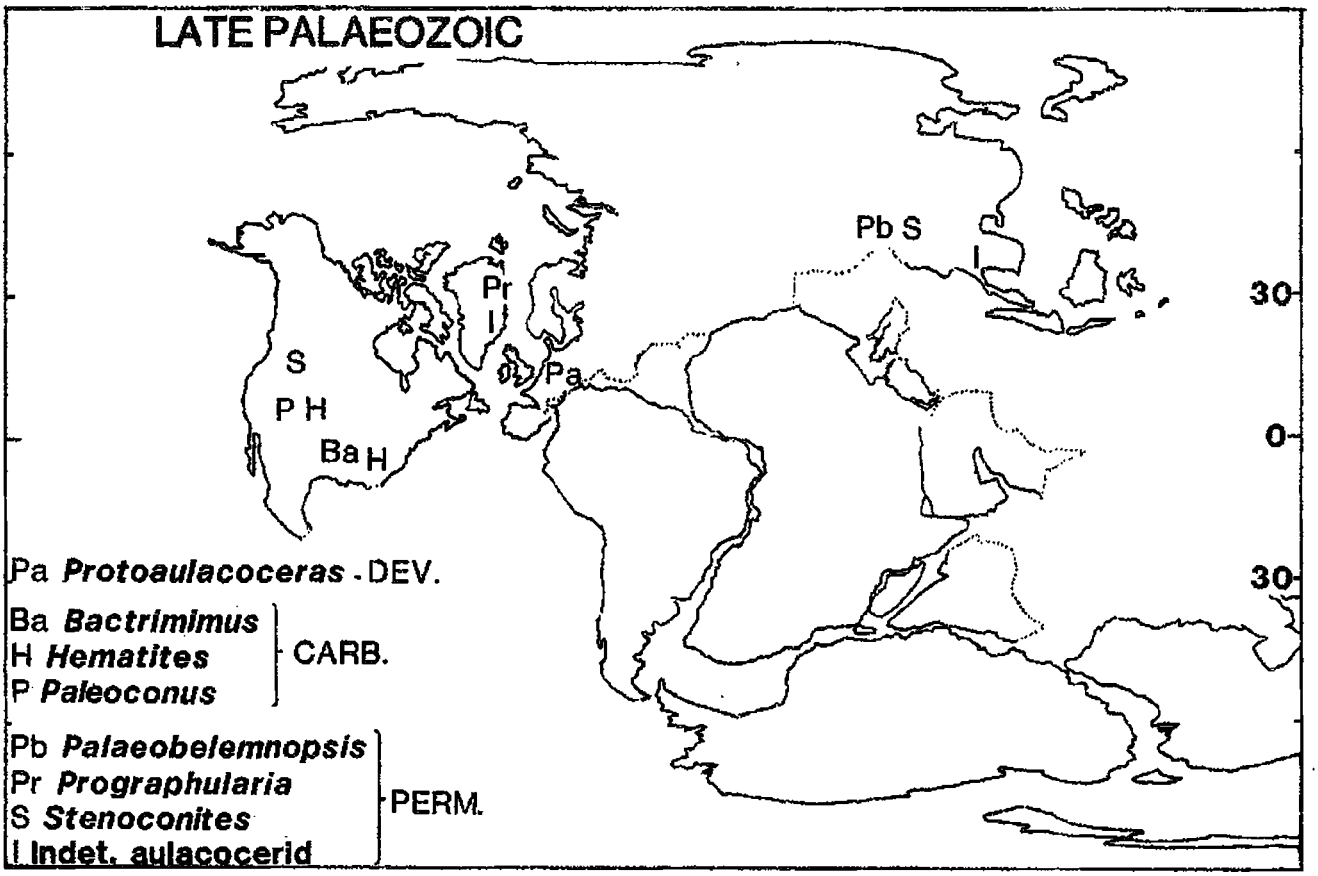


Fig. 2. Late Palaeozoic aulacocerid distributions. Base map from Smith *et al.* (1980, maps 53-54, late Permian). Dev., Devonian; Carb., Carboniferous; Per., Permian. Localities discussed in text. For *Bactrimimus* , read *Bactritimimus*.

rences in North America, China, India and Europe. The Xiphoteuthididae first appeared at this time, and were apparently more common than the Aulacoceratidae, which had continued from the Palaeozoic. However, this pattern of replacement by the Xiphoteuthididae may be an artifact, due to imperfect records, as by late Triassic times this trend was reversed, with a larger number of aulacoceratid than xiphoteuthid species. *Atractites* is the dominant xiphoteuthid genus in Middle Triassic sediments, several species being recorded from Europe (e.g. Mojsisovics, 1882; Salomon, 1895; Tommasi, 1889; Martelli, 1904), Turkey (Toula, 1896), Nevada (Smith, 1914; Silberling & Nichols, 1982), Spitsbergen (Spath, 1921, BMNH C. 27278-79), the Himalayas (Diener, 1907, 1908), with a more dubious record from the Chinese-Vietnamese border (Mansuy, 1912). *Mojsisovicsteuthis* first appeared in Middle Triassic and is known mainly from Alpine regions (e.g. the conical *Atractites* phragmocones of Mojsisovics, 1882; Salomon 1895; Tommasi, 1899). It is possible that some of the taxa attributed to this genus by Rieber (1973) might be more properly refered to *Zugmontites*, a genus characterised by a compressed and incurved phragmocone, that was first recorded from the Middle Triassic (lower Muschelkalke) of southern Germany (Reis, 1907). A single dubious specimen possibly referable to *Mojsisovicsteuthis* was recorded (as *Atractites* sp. ind.) from Siberia by Mojsisovics (1886). *Calliconites* first appeared at this time, and several specimens probably conspecific with those of the Upper Triassic of Timor (e.g. *C. gracilis* (v. Bülow)) are in the GSC collections from the Ladinian of British Columbia (Monkman Pass, GSC loc. 83862; Alaska Highway GSC loc. 98901). In addition, the specimens of *Atractites nevadensis* Meek illustrated by Silberling & Nichols (1982) are similar to later Triassic examples of *Calliconites* from Sicily (Gemmellaro, 1904) and Timor (v. Bülow, 1915). In contrast to this domination by the Xiphoteuthididae, the only record of an aulacoceratid genus at this time is a single, dubious juvenile specimen from Romania assigned to *Dictyoconites (Dictyoconites kongazensis* Kittl) by Kittl (1908).

There are much more data available for Upper Triassic aulacocerid occurrences, especially from classic areas such as Timor and the Alpine region of Europe. Both the Aulacoceratidae and the Xiphoteuthididae were common and diverse at this time. However, with some exceptions, the Aulacoceratidae were largely restricted to the Tethyan zone, the genera *Aulacoceras* and *Dictyoconites* being common in Austria and Italy, the former genus also being recorded from Cyprus (Henson *et al.*, 1949; specimen BMNH C. 46512, close to *A. sulcatum* Hauer) and Turkey (Dauphin, 1982, 1983). In addition to these Mediterranean records, the *Aulacoceratidae* are known in the In-

donesian Archipelago, where *Aulacoceras* and *Buelowiteuthis* (= *Dictyoconites sensu* v. Bülow, 1915) are very common (v. Bülow, 1915), and Tibet, where *Aulacoceras* conspecific with Timor examples have been found (Chen, 1982). *Buelowiteuthis* is most diverse in Timor (6 species, see v. Bülow, 1915 and Jeletzky, 1966), but there are isolated examples outside this region. Thus there is one species known from Europe, *B. geyeri* (Diener, 1919) (incorrectly recorded as *B. kittli* by Jeletzky, 1966, p. 25), one from the Himalayas (Diener, 1908, recorded as *Dictyoconites* sp. ind. aff. *haueri*), and another from British Columbia (*B. plana* (v. Bülow, 1915); see Jeletzky, 1966, p. 25, pl. 18, fig. 1).

'True' *Dictyoconites* is unknown in Indonesia and is largely endemic to the Mediteranean Tethys (e.g. Mojsisovics, 1882). However, fragments of this genus have been recorded from Mexico (Sonora, Mina el Antimonio) (Miller, 1961) and I have examined topotypes (no. 6533, several specimens) from the Peabody Museum collections, Yale University (on loan to Dr J.A. Jeletzky, GSC) confirming this record. A single fragmentary specimen of *Dictyoconites* from the Peace River Foothills (GSC loc. 9646), British Columbia is in the GSC collections. However, Smith's (1927) record of this genus from California is referable to *Aulacoceras* (J.A. Jeletzky pers. comm., 1987). *Aulacoceras* species conspecific with those of Timor and Europe (e.g. *Aulacoceras sulcatum* Hauer) are also represented in British Columbia, from McConnel Creek (GSC locality 93555), Vancouver Island (GSC loc. 17388), Toad River (GSC loc. 86182), Telegraph Creek (GCS locs 32777, 32820), Quadra Island (GSC loc. 22692) and Harrison Lake (GSC. loc. 40435). *Aulacoceras carlotense* Whiteaves (Holotype GSC 4749) from the Queen Charlotte Islands is a poorly preserved mould of a probable juvenile *Aulacoceras sulcatum* (Whiteaves, 1887).

The genus *Prographularia*, first recorded from the Permian of Greenland, is also present in the Upper Triassic sediments of Austria (see Jeletzky & Zapfe, 1967), New Zealand (= *Aulacoceras* of Trechmann, 1918, BMNH C. 21944; see also Marwick, 1953), Japan (= *Dictyoconites nipponicus* of Shimizu & Mabuti, 1940), and in collections of Upper Triassic aulacocerids from Timor (Oi Batok) on loan to Dr J.A. Jeletzky (GSC). Appearing of the first time in the late Triassic is *Belemnococeras*, a distinct, almost smooth aulacoceratid with a distribution apparently restricted to the Arctic basin. It was first recorded from the Upper Triassic of Siberia (Kharaulakh Mountains) by Popov (1964) and Dagys & Nal'nyaeva (1987), but also occurs in sediments of similar age in the Canadian Arctic (Axel Heiburg Island, GSC locs 26168, 26373). *Austroteuthis*, a related genus, is so far known only from the Upper Triassic of Austria (Fischerweise; see Jeletzky & Zapfe, 1967).

The Xiphoteuthididae were less common than the Aulacoceratidae in the late Triassic, but nontheless are equally widespread. *Atractites* is the most widely recorded, occurring in the Alpine regions (e.g. Mojsisovics, 1882),

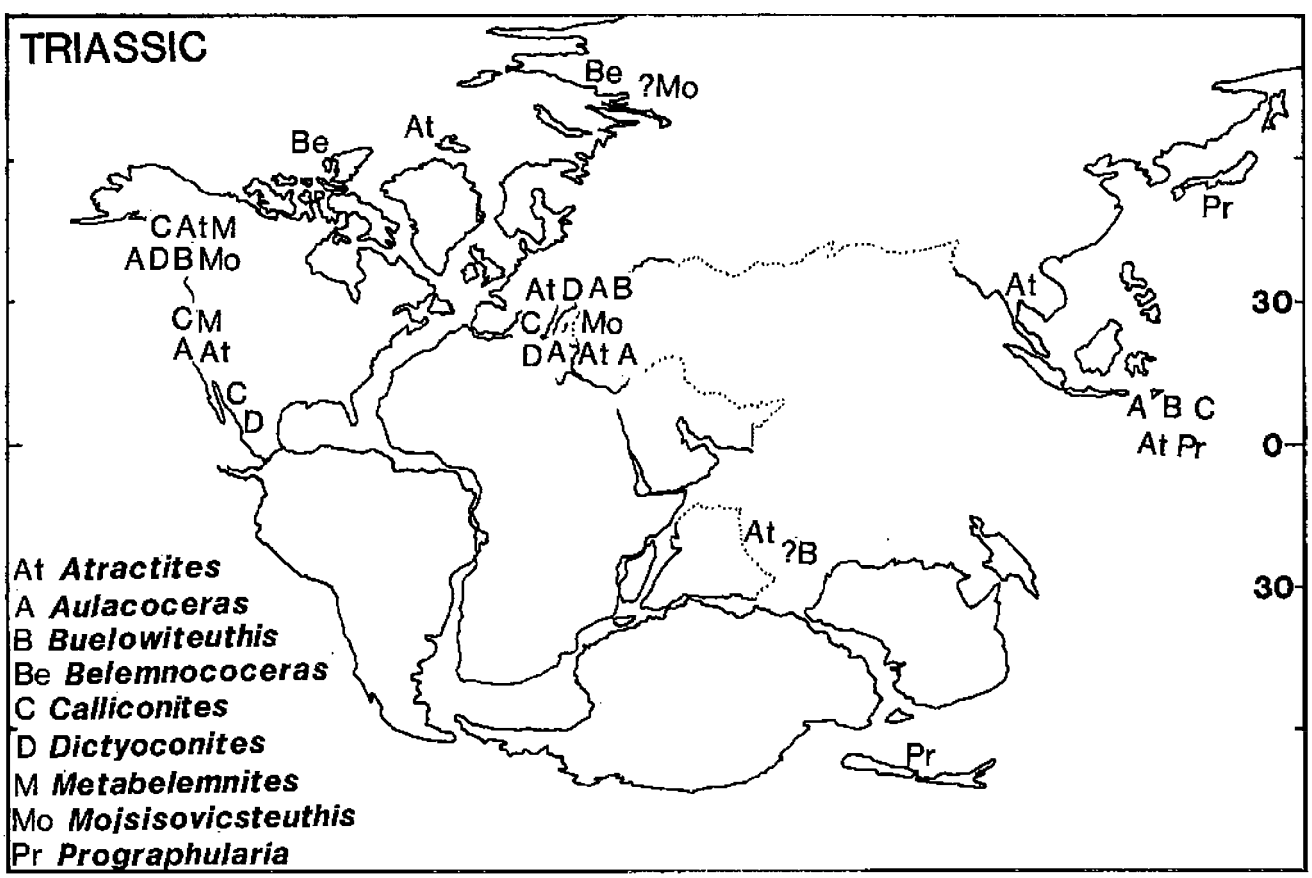


Fig. 3. Generalised mid and late Triassic aulacocerid distributions. Base map from Smith *et al.* (1980, maps 45-46). Cordillierran (and other) Terranes unreconstructed (see Tozer, 1982). Localities discussed in text.

Greece (Renz 1911), Nevada and Mexico (recorded as *Choanoteuthis*, Fischer, 1951; Miller 1961). In addition, Chen (1982) records five species of *Atractites* from Tibet, although it is possible that two of these represent *Mojsisovicsteuthis*. Finally, *Atractites (A. otapiriensis*, see Thomson, 1913, p. 33) has been recorded from the Upper Triassic (Otapirian) of New Zealand (Hector, 1878; Thomson, 1913), although later authors have assigned these specimens to *Aulacoceras*. Closely related to *Atractites*, and appearing for the first time, is *Metabelemnites*, recorded from California (Smith, 1927) and British Columbia (Jeletzky, 1966). This genus is relatively common in the Upper Triassic sediments of British Columbia, and there are specimens in the GSC collections from Peace River (GSC loc. 83826), Toad River (GSC loc. 42398), Hamilton Lake (GSC loc. 90796), Baldy Hill (GSC loc. 9381) and Mount Knidle (GSC loc. 42377). *Calliconites* has been recorded from Sicily (Gemmellaro, 1904) and Timor (v. Bülow, 1915; Jeletzky, 1966). Miller (1961) recorded *?Metabelemnites* in a 'battlefield' accumulation from the Upper Triassic of Sonora (Mexico). Examination of topotype material on loan to Dr J.A. Jeletzky (GSC) from the Peabody Museum, Yale University (no. 6533) reveals that these rostra bear the typical groove pattern of *Calliconites*. This genus is also found in British Columbia (Toad River area GSC locs 13248, 68180), and a single specimen is recorded from California (as *'Atractites' drakei* Smith, 1927). Finally, *Mojsisovicsteuthis* has been recorded from Austria (Mojsisovics, 1882, 1902) and possibly occurs in Sicily (Gemmellaro, 1904).

In summary, the Triassic was a time of maximum development for the Aulacocerida. There are little data available for the early Triassic, but in the mid-Triassic the Xiphoteuthididae, appearing for the first time, were dominant over the much older Aulacoceratidae. This position was reversed in the late Triassic when the Aulacoceratidae were once again in the ascendancy. The Xiphoteuthididae were reasonably widespread in the mid-Triassic and examples are found in North America, Spitsbergen, the Mediteranean Tethys and the Himalayas. In the late Triassic, the Xiphoteuthididae maintained their distribution, and examples are known from North America, Siberia, the Mediteranean Tethys, Indonesia and possibly New Zealand. The Aulacoceratidae were in the main restricted to Tethys, with two distinct regions of endemism. The first is represented by the Mediteranean Tethys with *Dictyoconites*, the second, by the Indonesian Archipelago with *Buelowiteuthis*. In both these regions, *Aulacoceras* is dominant, and often the same species can be recognised throughout. In North America, *Aulacoceras*, *Buelowiteuthis* and *Dictyoconites* have been recorded in British Columbia and California (Whiteaves, 1887; Smith, 1927; Jeletzky, 1966).

3. *Jurassic records* (text-fig. 4). There are several records of Jurassic Aulacocerida, especially in the Lower Jurassic. Lower Jurassic sediments yield only xiphoteuthids, as no aulacoceratids have been found in rocks younger than the Upper Triassic (the *Aulacoceras* cited by Jenkyns *et al.*, 1985 from Switzerland are more properly assigned to *Atractites?*; M.K. Howarth, pers. comm., 1987). *Atractites* is again the dominant genus, widespread in the Pliensbachian-Toarcian of the Mediteranean Tethys (e.g. see Bülow-Trummer, 1920), including Italy (Meneghini, 1867); Spain (Melendez, 1947), Hungary (BMNH C. 46833-34, from near Verzprém), the Caucasus (Nutsubidze, 1966), Turkey and Iran (personal observation), as well as occuring in southern Germany (Quenstedt, 1846-49), France (Mattéi *et. al.*, 1987) and more rarely, in southern England (Huxley, 1864; Müller-Stoll, 1936; Jeletzky, 1966). *Atractites* (and related, probably new, taxa; A. v. Hillebrandt pers. comm., 1987) are found in the Pliensbachian-Toarcian of South America (Tilman, 1917; Hillebrandt & Schmidt-Effing, 1981; Hallam, 1983), as well as possibly in the Toarcian (Ururoan) of New Zealand (Grant-Mackie, 1959, p. 558; Stevens, 1965, p. 66). In North America, *Atractites* is common in the Sinemurian-Pliensbachian (Frebold, 1969) where large hastate individuals are common in the Fernie Formation of Alberta. *Mojsisovicsteuthis* also survived into the early Jurassic, and it is known in association with *Atractites* (Savi & Meneghini, 1850; Meneghini, 1867) in the Hettangian to Toarcian of Italy (La Spezia) and the Mediteranean Tethys. The only new aulacocerid genus to appear in the Jurassic is *Chitinoteuthis* Müller-Stoll, which is unique in possessing a largely organic rostrum, but with a typical aulacocerid phragmocone warranting a separate family, the Chitinoteuthididae. So far it is known only from the Domerian of Germany (Müller-Stoll, 1936).

In many of these regions xiphoteuthids occur in association with 'true' belemnites (Belemnitina), which appeared in the earliest Jurassic (see Doyle, 1987). Thus in Turkey numerous *Atractites* occur with a rich belemnitid fauna comprising the genera *Passaloteuthis*, *Angeloteuthis* and *Pseudohastites* of early Pliensbachian age, while in northwest Europe rarer *Atractites* (e.g. *Atractites elongata* (de la Beche)) existed with similar belemnitids in the later Pliensbachian (Huxley, 1864) suggesting there was little competition between them. However, Hallam (1983) and A. v. Hillebrandt (pers. comm., 1987) have pointed out that although true belemnites are absent in South America, xiphoteuthids are common, and in North America, the xiphoteuthids are replaced in the Toarcian by an influx of belemnitids (J.A. Jeletzky pers. comm., 1987). After the early Jurassic there are few records of xiphoteuthids, only a single species being recorded from the Oxfordian of France (Dreyfuss, 1957), its recognition being based upon its shallow apical angle and relatively high camerae. A similar aulacocerid-like coleoid phragmocone is known from the Lower Cretaceous of Zululand, southern Africa (W.J. Kennedy collection, Oxford University Museum). However, it is more likely that this phragmocone is a representative of another coleoid (a groenlandibelid for instance), rather than a 'younger' aulacocerid.

In summary, the aulacocerids survived into the Jurassic represented only by the family Xiphoteuthididae with the genera *Atractites* and *Mojsisovicsteuthis*, and by the rare monotypic family Chitinoteuthididae which appeared in the Domerian. The xiphoteuthids were common only in the Tethyan regions in the early Jurassic, mainly in Mediteranean Tethys, but also in South America and possibly New Zealand. However, isolated species (e.g. *Atractites elongata* (de la Beche); *A. alveolaris* (Quenstedt)) did penetrate as far north as northwest Europe. In the early Jurassic the belemnites first appeared, and were apparently able to co-exist alongside the aulacocerids in Tethys and elsewhere, although generally with greater diver-

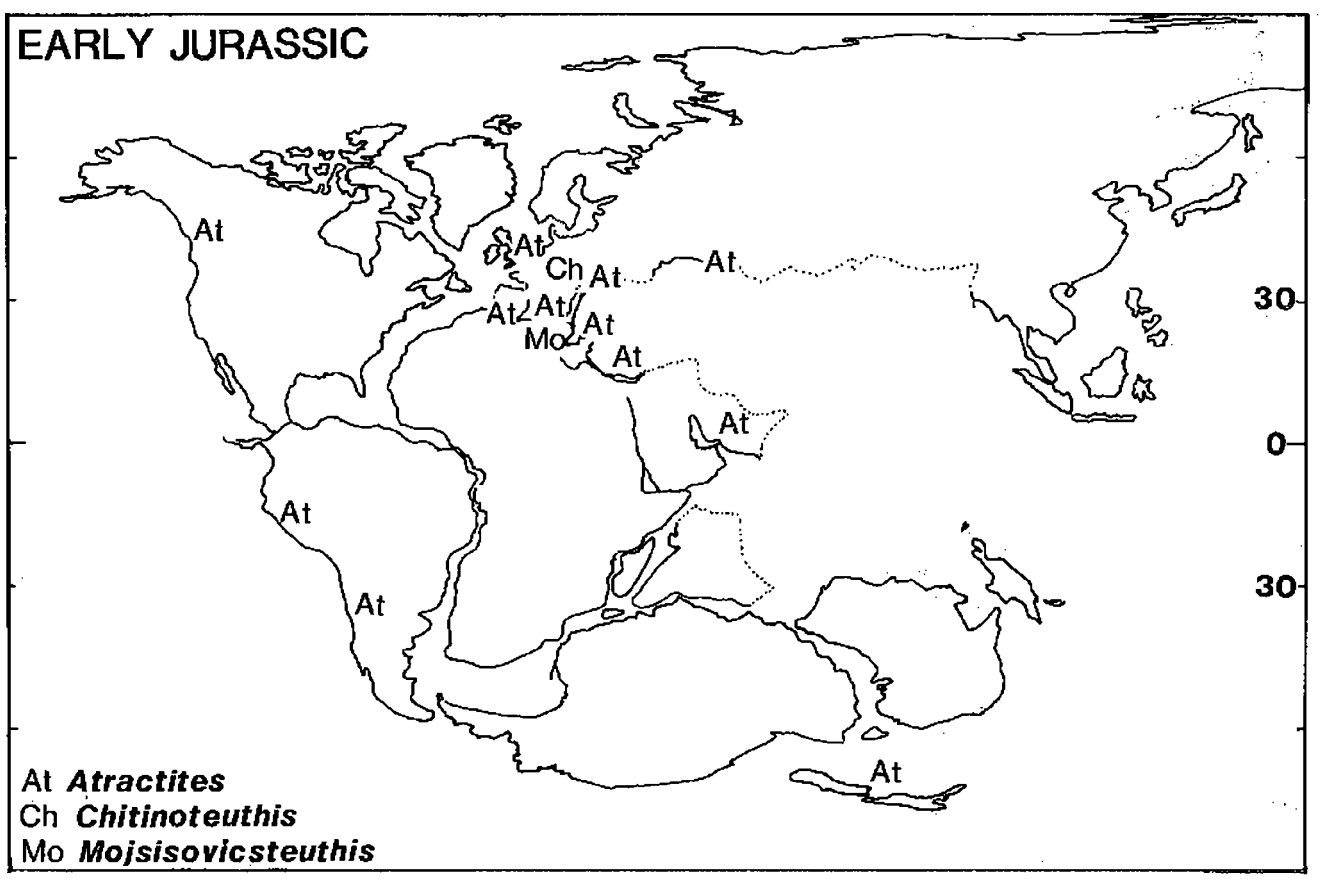
sity. However, in some regions, aulacocerids were able to remain dominant until replaced by belemnitids in the later early Jurassic (in South America for example). Aulacocerids are uncommon in post-Lower Jurassic sediments, the last recorded example being known from the Oxfordian (late Jurassic) of southern France.

DISCUSSION

Little can be drawn from the sparse records of Palaeozoic aulacocerids save to illustrate that the forerunners of the more abundant Triassic aulacocerids had already appeared in the Carboniferous and Permian. However, the occurrence of aulacocerids in the Permian of Thailand and Nevada is consistent with the low-latitude distribution of their Triassic descendants, although the occurrence of *Prographularia* in Greenland at this time is puzzling in the light of its purely Tethyan-zone distribution in the Triassic.

Mid to late Triassic aulacocerids are well-represented in the record, and indicate a broad pattern of relatively low latitude, 'Tethyan-zone', distribution. Both Aulacoceratidae and Xiphoteuthididae are broadly distributed within Tethys (land-locked to the north), and occur at similar latitudes on the other side of the palaeo-Pacific (Panthalassa) in the Western Cordillierran terranes (e.g. Wrangellia, Quesnella, etc) which apparently formed an archipelago of islands at lower latitudes than their position today in western Canada and USA (Tozer, 1982). Thus *Aulacoceras, Calliconites, Mojsisovicsteuthis* and *Atractites* are recorded from most Tethyan areas (e.g. southern Europe, the Balkan region, Turkey, the Himalayas), Timor (also in Tethyan latitudes; Tozer, 1982, fig. 2) as well as British Columbia, California, Nevada and Sonora, Mexico. Indeed, species of these genera are often identical in these areas, for example *Aulacoceras sulcatum* Hauer occurs in Europe, Turkey, Timor and British Columbia. Triassic *Prographularia*, as yet un recorded in North America, is also known from the Tethyan latitudes, recorded from Austria, Timor, New Zealand and Japan (see Tozer, 1982, fig. 2). The broadly Tethyan distribution of the Aulacocerida in the Trias does not necessarily imply climatic control, especially in the warm, equable Trias (Frakes, 1979). Tethys had no outlet to the north or west due to widespread regression in the Trias (Howarth, 1981; Tozer, 1982), allowing easy migration only to the east. This is consistent with the broad correspondance of aulacocerid faunas between Tethys and the Western Cordillierran terranes at this time (text-fig. 3).

Some endemism was present within the broad Tethyan belt; *Buelowiteuthis* is largely restricted to Timor, although with isolated examples in Tethys and British Columbia, while *Dictyoconites* is unknown in Timor, being common in western Tethys and recorded from British Columbia. Another example is *Metabelemnites* which was apparently restricted to the shoal of islands off the coast of North America in the Triassic. In addition, there are some aulacocerids recorded from outside the Tethyan latitudes; they include *Belemnococeras*, endemic to the Kharaulakh Mountains of Siberia and Axel Heiberg Island (Arctic Canada), and the isolated records of *Atrac-*



Text-fig. 4. Generalised early Jurassic aulacocerid distributions. Base map from Smith *et al.* (1980, maps 41-42). Cordillierran (and other) Terranes unreconstructed. Localities discussed in text.

tites from Svalbard, and *?Mojsisovcsteuthis* from Siberia. Possibly these northern records represent migrants from the Western Cordillierran region (see Howarth, 1981, figs. 13.1, 13.3).

In the early Jurassic, the Aulacoceratidae had disappeared, leaving the Xiphoteuthididae. This family continued to be common only in the Tethyan belt, but probably due to the early Jurassic transgressive phase, *Atractites* was able to penetrate into northwest Europe. *Atractites* was also widespread in the Americas, occurring in the Western Cordillierra and farther south in South America. The xiphoteuthids were able to mix freely with the now diverse belemnitids in Tethys and Europe, although they remained dominant in regions such as British Columbia and South America until they were replaced by an influx of belemnitids in the Toarcian.

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